MACROPSYLLA NOVAEHOLLANDIAE (SIPHONAPTERA: HYSTRICHOPSYLLIDAE), A NEW SPECIES OF FLEA FROM TASMANIA

Michael W. Hastriter and Michael F. Whiting

(MWH) Monte L. Bean Life Science Museum, Brigham Young University, 290 MLBM, P.O. Box 20200, Provo, UT 84602-0200, U.S.A. (e-mail: hastritermw@sprintmail.com); (MFW) Department of Zoology, 574 Widtsoe Building, Brigham Young University, Provo, UT 84602, U.S.A.

Abstract.—A **new species** of flea of the family Hystrichopsyllidae, ***Macropsylla novaehollandiae* Hastriter**, collected from *Pseudomys novaehollandiae* Waterhouse near Coles Bay, Tasmania, is described. The familial placement of the genus *Macropsylla* Rothschild and *Stephanopsylla* Rothschild are discussed.

Key Words: flea, Hystrichopsyllidae, *Macropsylla*, *Stephanopsylla*, Tasmania

Fleas recently collected from small mammals in northeastern Tasmania were initially thought to represent *Macropsylla hercules* Rothschild. Further study revealed that they represent an undescribed species. Rather common in eastern Australia, the nominate species, *M. hercules*, was described from two females, individually collected from *Mus velutinus* = *Rattus lutreolus* (J. E. Gray) and an unidentified species of *Mus* from Launceston, Tasmania. Hopkins and Rothschild (1956) later illustrated the male head and genitalia of *M. hercules* from Emerald, Victoria, Australia and provided a brief description. The purpose of this paper is to describe a new species of *Macropsylla* and provide supportive evidence for the familial placement of this unique genus.

MATERIALS AND METHODS

The overall body dimensions of males and females were measured from the foremost portion of the frons to the apex of the st. VIII in males and to the posterior border of the sensilium in females. Illustrations were prepared from digitized images prepared with a Zeiss Stemi SV 11 dissecting microscope and Dage-MTI digital camera. Terminology of morphological structures follows those of Rothschild and Traub (1971).

Macropsylla hercules Rothschild 1905
(Figs. 4, 5, 8–12, 14, 16, 17)

Material examined.—AUSTRALIA, New South Wales: ex *Rattus assimilis* = *Rattus fuscipes* (Waterhouse), 24 ♂, 32 ♀; ex *Rattus rattus* (L.), 3 ♂, 3 ♀; ex *R. fuscipes*, 2 ♂, 2 ♀; ex *R. lutreolus*, 3 ♂, 2 ♀, and ex *Melomys* sp., 1 ♀. Northern Territory: ex *Melomys littoralis* = *Melomys burtoni* (Ramsay), 1 ♀. Queensland: ex *R. fuscipes*, 12 ♂, 24 ♀; ex *R. assimilis*, 1 ♂, 2 ♀; ex *Parameles nasuta* E. Geoffroy, 3 ♀; ex *Rattus* sp., 2 ♂, 1 ♀, and *Melomys* sp., 1 ♀. South Australia (Kangaroo Island): ex *R. fuscipes*, 8 ♂, 6 ♀. South Australia (mainland): *R. fuscipes*, 1 ♂. Tasmania: ex *R. lutreolus*, 20 ♂, 21 ♀; *Pseudomys higginsi* (Trouessart), 1 ♂, 4 ♀; ex *Rattus lutreolus velutinus* = *R. lutreolus*, 1 ♂; ex *Mus velutinus* = *R. lutreolus*, 1 ♀ (lectotype), and ex *Mus* sp., 1 ♀ (paralectotype). West Head (location unknown): ex *R. fus-*

cipes, 1 ♂. Victoria: ex *R. assimilis*, 11 ♂, 4 ♀; ex *Mus assimilis* = *R. fuscipes*, 8 ♂, 5 ♀; ex *R. lutreolus* or *R. assimilis*, 9 ♀; and ex *R. lutreolus*, 1 ♀.

Remarks.—Rothschild (1905) indicated in his original description of *M. hercules* (based on two females) that the row of marginal spinelets on t. V is interrupted dorsally. Examination of the lectotype reveals that the dorsal spinelets are not interrupted, but broken off (Figs. 6, 12, black arrows), although those of the paralectotype are interrupted (Fig. 9, black arrow). A dorsal interruption in the row of marginal spinelets among the 223 specimens (98 ♂, 125 ♀) examined was present in only a few specimens from three collection localities. Three females from Kosciusko National Park, New South Wales possessed a broad interruption in rows on t. III–V. No males were examined from that locality. A slight dorsal interruption was also present on t. V of a single male from the Kuipto Forest, just south of Adelaide, South Australia. This male also possesses four deformed setae (much longer than normal spinelets, or combs), two each on one side arising from the base of t. VI and t. VII, respectively. The entire series (8 ♂, 6 ♀) from Kangaroo Island (just south of the locality of the specimen from Kuipto Forest) possess a dorsally interrupted row on t. V in addition to an interrupted row on t. VI (numbering 5–10 spinelets per side). Excluding the new species herein described, the rows of marginal spinelets on t-II-V of all specimens examined from Tasmania (22 ♂, 27 ♀) were complete, and supernumary setae were not present on t.-VI. Considerable variation exists in the number of marginal spinelets in each row; however, the number of spinelets occurring at, or below the level of the spiracle on t. V is consistent, ranging from 4–8 in males and females of *M. hercules* and 0–1 in the new species (Figs. 6–11, white arrows denote position of spiracles).

A new unpublished record of *M. hercules* was examined (National Museum of Natural History, Smithsonian Institution, Wash-ington, DC) from *M. littoralis* = *M. burtoni*, Arnhem, Smith Point, Caberg Peninsula, Northern Territory, 25 June 1978, leg. P.R. Bavorstock, extending the northern limits of the species to the north central coast of Australia. *Rattus fuscipes* and *R. lutreolus* are the usual hosts of this flea, but neither is normally found on the northern coastal areas of Australia [Wilson and Reeder (1993)]. Perhaps these commensal rodents have been introduced by commerce along the coast of the Arnhem region, transporting the flea with them. The occurrence of *M. hercules* on *M. burtoni* is probably an accidental association with *R. fuscipes* or *R. lutreolus*.

Macropsylla novaehollandiae Hastriter, new species
(Figs. 1–3, 6, 7, 13, 15)

Type material.—AUSTRALIA. ♂ holotype, ♀ allotype, 2 ♀ paratypes, ex: *Pseudomys novaehollandiae* Waterhouse, Coles Bay, Tasmania, 25 November 1998, B. Lazenby; and 1 ♀ paratype, ex: *P. novaehollandiae*, Flinder's Island, Tasmania, 5 January 1999, B. Lazenby. Holotype, allotype and two paratypes deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, and one paratype in the collection of the senior author.

Diagnosis.—Males may be distinguished from *M. hercules* by the length of the sclerotized inner tube that is obviously longer and wider than the spatulate spiniform of the basimere (Fig. 1), the apico-lateral surface of P2 is adorned with 9–10 blunt spiniform setae (14–19 in *M. hercules*) (Fig. 4), spinelets of t. V interrupted dorsally (Fig. 6, black arrow), no more than 1–2 marginal spinelets below level of spiracle on t. V (Fig. 6, white arrow), and st. IX is without a distinct sinus in the caudal margin beneath a caudally pointed acute lobe (compare Fig. 1 and 4). Females are very similar to *M. hercules*, but may be separated by a combination of the following characters: 1) a much weaker lobe along the posterior margin of st. VII, 2) anterior row of setae
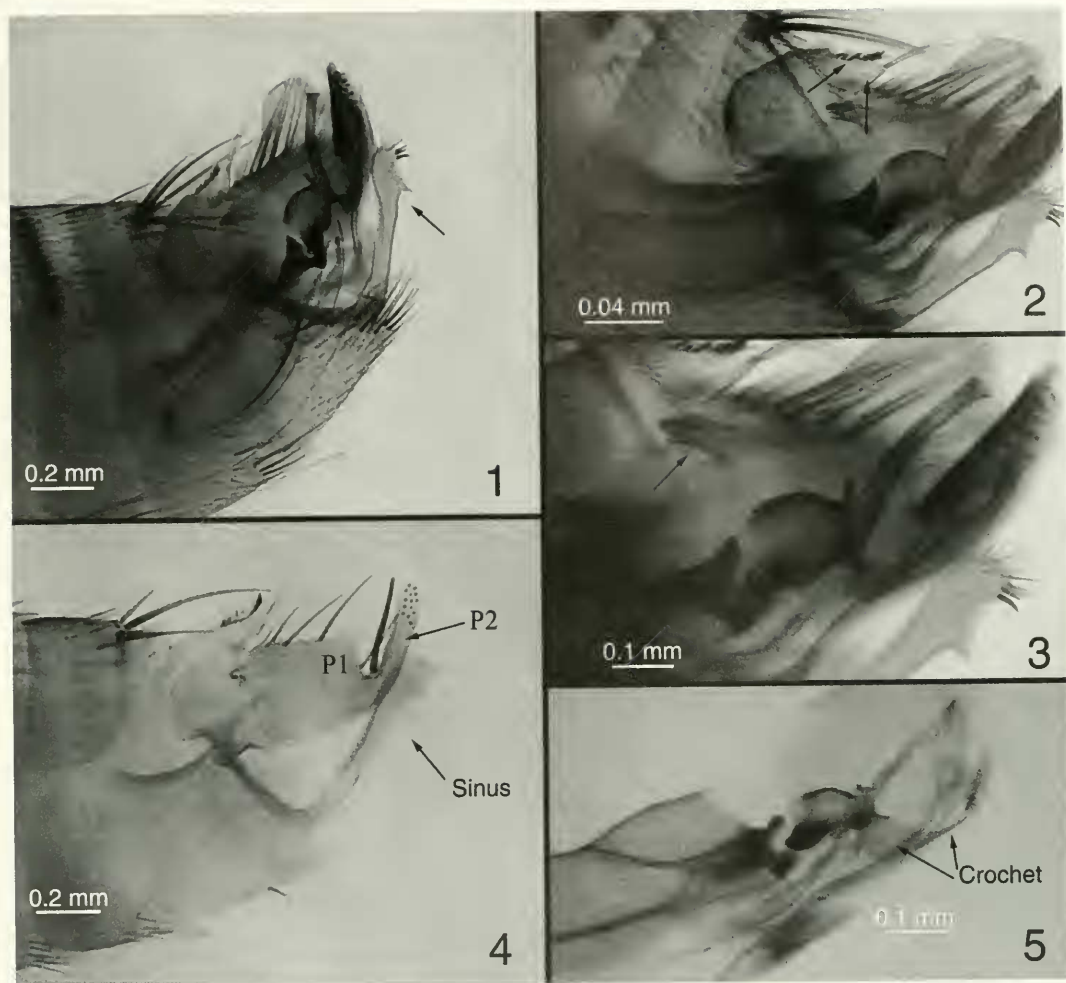
Figs. 1–5. 1–3, *Macropsylla novaehollandiae* (male), Coles Bay, Tasmania. 1, Terminal segments (arrow denotes lack of sinus on sternum IX). 2, Aedeagus (arrows denote dorsal and vental anal lobes). 3, Apex of aedeagus (note relative size of sclerotized inner tube and spatulate spiniform on basimere). 4–5, *M. hercules* (male), Pearl Beach, New South Wales. 4 Terminal segments with right side and aedeagus removed (P1/P2 = processes 1 and 2 of basimere; sinus on caudal margin of sternum IX). 5, Terminal aspect of aedeagus (note relative size of sclerotized inner tubes of Figs. 3 and 5).

on t. VII much finer and curving strongly caudad below level of spiracle (Fig. 7), 3) dorsal antesensilial bristle ¾ or more the length of the middle bristle (only ½ in *M. hercules*), 4) sclerite in dorsal wall of oviduct larger and expanded dorsally (triangular vs. rectangular) (Figs. 13–14), and 5) a combination of marginal spinelets on t. V interrupted dorsally with no more than one spinelet extending below level of spiracle (Fig. 7, white arrow).

Description.—*Head:* Clear marginal band running parallel with frons and diverging dorsad, without setation. Narrow pale marginal band parallel with frons. Six large setae and patch of smaller setae adorn preantennal area in a random pattern in addition to numerous minute scattered setae. Eye well developed, notched ventrally, situated dorsad of angled row of 9 broad spatulate genal ctenidia. Anterior arm of tentorium visible well below eye and anterior
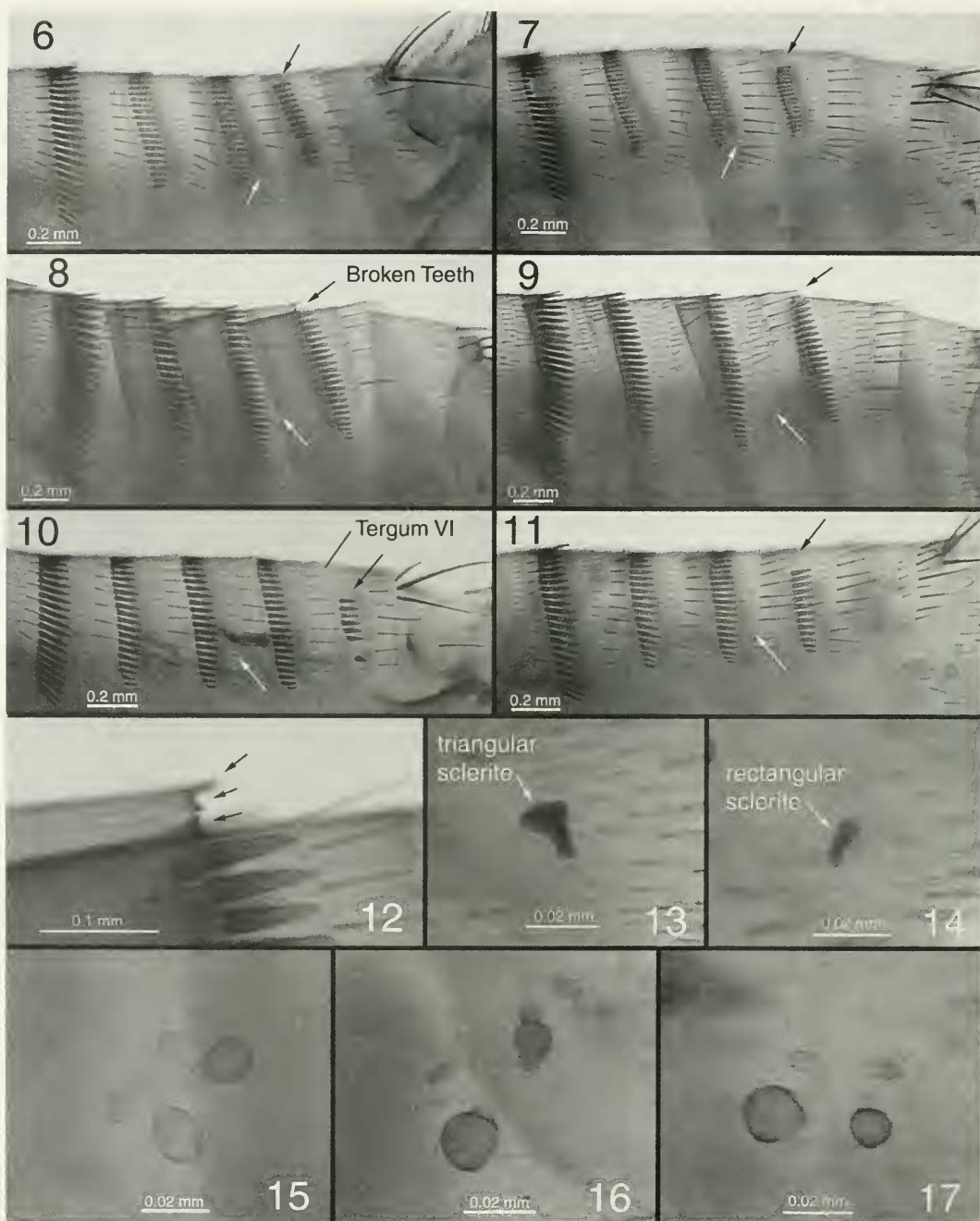
Figs. 6–17.   6–7, *Macrosylla novaehollandiae* (male holotype, female allotype, respectively, Coles Bay, Tasmania). 8–9, *M. hercules* (female lectotype, female paralectotype, Launceston, Tasmania). 10–11, *M. hercules* (females), Kangaroo Island, Australia. 12, *M. hercules,* enlargement of broken teeth noted in Fig. 8. 13, *M. novaehollandiae* (allotype), sclerite of bursa copulatrix. 14, *M. hercules,* sclerite of bursa copulatrix. 15, *M. novaehollandiae* (allotype), spermathecae. 16–17, *M. hercules.* 16, Spermathecae (lectotype). 17, Spermathecae (Kangaroo Island).

to genal ctenidia, central internal oral tuber arising from oral angle. Antenna of male extending onto prosternum, some setae on pedicel extending about half length of antenna. Female antenna not extending to prosternum and longer setae of pedicel extending nearly to apex of antenna. Postantennal region with two defined rows of setae, with anterior setae somewhat scattered. Row of 10–13 slender setae along dorsal margin of antennal fossa. Distinct suture separating preantennal and postantennal areas. Internal occipital tuber present. Maxillary palpus 5-segmented in both sexes, labial palpus 8-segmented in male and 9-segmented in female extending just short of apex of coxae. Maxillary lobe sharply acute at apex. Internal apodeme connecting head to thorax extending deep into prothorax. *Thorax:* Three rows of setae on prothorax and pronotal comb of 15–16 teeth per side in both sexes. Proepisternum with dorsal depression on male to accommodate clavus of antenna, less pronounced in female. Meso- and metanota with 5 rows of setae, each row diminishing in size cephalad. Mesepimeron and mesepisternum with many scattered setae, pleural rod stout and bifurcate dorsally. Lateral metanotal area with 7 scattered setae in male and 3 vertical rows (2, 4, 3–4 setae, anterior to posterior) in female. Pleural arch well-developed, dorsal portion heavily sclerotized. Metepisternum bearing 2 moderate setae dorsally, metepisternum fusing with that of other side and protruding downward between coxae. Metepimeron with 3 vertical rows of setae, posterior stoutest and most dorsal seta below level of spiracle. *Legs:* Lateral surface of forecoxa heavily setose, mesal surface reticulated without setae. Mid- and hindcoxae with sparse small setae along anterior lateral and mesal margins. Oblique sulcus of midcoxa complete. Two femoral pit guard hairs on each femur, each about equal in size on mid- and hindfemora, medial smaller on forefemur (see Remarks). Numerous lateral setae found on all femora and only 2–3 setae on mesal surface of

each. Each femur with coarse surface reticulations. Lateral bristles guarding femoral-tibial joints longest of pair on forefemur and shortest on mid- and hindfemora. Dorsal margin of foretibia adorned with many heavy long spines (one nearly reaching apex of second tarsal segment) resembling a false comb; mid- and hindtibiae with 7 and 8 dorsal notches, respectively, with additional setae interspersed between notches. Mesal surface of mid- and hindtibiae sculptured with triangular scalelike reticulations. Hindtibia with apical tooth. Segment I of hindtarsus about as long as hindtibia and segment II longer than segments III and IV combined. Fifth tarsal segment of each leg adorned with a complex set of lateral plantar bristles; first pair set onto plantar surface positioned between second pair, third and fourth pairs each with two bristles per side. Each plantar surface with many minute setae and 2–4 (variable) preapical plantar bristles (some spiniform). *Unmodified abdominal segments:* Chaetotaxy of t. I–VII variable. Only posterior main rows with intercalary setae. Tergites I–VI of male bears 3, 4, 4, 4, 4, and 3 rows, respectively and t. VII with a single defined row and numerous smaller setae scattered anteriorly. Female with similar pattern, but anterior rows less defined. Both sexes with marginal spinelets on t. II–V with row of spinelets interrupted dorsally on t. V. These total 46, 44, 36, and 30 (male), and 49, 44, 44–45, and 28–31 (female), respectively. Number of spinelets below level of spiracle on t. II–IV 7, 3, and 3 (male) and 6–8, 1–5, and 0–2 (female). Those situated below level of spiracle on t. V range from 0 to 2 in both sexes. Both sexes with 3 antesensilial bristles, ventral pair of equal length, and dorsal bristle ¾ as long as others. Abdominal st. II with a lateral patch of small setae (more numerous in female), and a single ventral seta per side; male with 5–7 stout setae per side in main rows and numerous scattered setae anterior to main row on st. III–VII, female same for st. III–VI. *Modified abdominal segments (male):* Tergum VIII re-

duced, covering little of terminal segments and bearing patch of fine setae across dorsum. Atrium of eighth spiracle greatly expanded, reminiscent of some species of *Megabothris* Jordan 1933. Basimere with two lobes (P1 and P2). P2 is highly modified immovable apical process (anatomically in usual position of the telomere) which bears 9–10 blunt spiniforms on mesal surface and single unique spatulate spiniform arising from sinus between the P1 and P2 (Figs. 1, 4). Located just below sensilium on basimere, 2 structures, which appear as vestigial telomeres, each with several slender setae apically (Fig. 3, arrow). Anterior portion of basimere heavily sclerotized. Sternum VIII with group of 9–10 stout setae per side near caudal margin with numerous smaller setae scattered over surface. Distal arm of st. IX uniquely fused into single structure (paired in most other genera of fleas) bifurcating at base into usual proximal arms. Apex of fused distal arms adorned with 6 spiniform setae and numerous stout setae. Caudal margin with beak-like process with margin below entire without indication of sinus (Fig. 1, arrow). Dorsal anal lobe studded with blunt spiniforn setae, ventral anal lobe bearing 2 long slender setae (Fig. 2, arrows). Many portions of aedeagus more highly sclerotized than those of other fleas, particularly sclerotized inner tube, crescent sclerite, crochet, and medial and lateral lobes of fulcrum. *Modified abdominal segments (female):* Three antesensilial bristles, dorsal bristle about ¾ length of middle bristle. Tergum VIII greatly expanded ventrally so as to envelop vestigial (membranous) st. VIII, covered with many setae, and those towards caudal margin more robust than those more anterior. Caudal margin forming angular lobe. Sensilial plate projecting anterior to caudal margin of t. VII, interrupting dorsal portion of t. VIII. Dorsal anal lobe much larger than inconspicuous reduced ventral anal lobe. Anal stylet nearly three times as long as wide, bearing single minute seta at base of long apical seta. Sternum VII without lobes or sinuses and st.

VIII vestigial. Paired spermathecae similar in size and much like those of *M. hercules* (Figs. 15–17). Hyperdeveloped trianglular sclerite in bursae copulatrix, rectangular in *M. hercules* (Figs. 13–14).

Size: Slide mounted specimens: male, 4.1 mm (n = 1), female, 4.5 mm (n = 2). Alcohol specimens: female, 3.3 mm (n = 2).

Etymology.—This species is named after the specific name of the host species, *Pseudomys novaehollandiae*, as a noun in apposition.

Remarks.—Nowak and Paradiso (1983) indicated that the New Holland mouse, *P. novaehollandiae* was limited to a few collections early in the 1900s from New South Wales to Mornington Peninsula of southern Victoria and from subfossil remains found in Tasmania until 1976 when Hocking (1980) reported a population on the northeastern coast of Tasmania. *Macropsylla hercules* is commonly found throughout eastern Australia from Queensland to South Australia and Tasmania on a variety of murid hosts, none of which include *P. novaehollandiae*. The rarity of collecting *P. novaehollandiae* (to include its ectoparasites) probably accounts for the failure to previously find this new species of flea. Additonal collection of this endangered host species on mainland Australia will predictably yield additional specimens of *M. novaehollandiae*.

A pit located on the ventral anterior margin of the femora of each leg has previously not been reported. Although the function of this pit is not known, it appears to be present on most, if not all species of fleas. Dorsad to the "pit" are two stout setae that project downward over the "pit" so as to shield the underlying "pit" structure. The size and arrangement of these setae are variable from species to species and may be consistent among different families. The details and significance of this new observation will be published elsewhere.

DISCUSSION

Oudemans (1909) placed *Macropsylla* in a separate subfamily (Macropsyllinae) and family (Macropsyllidae) based on the presence of an internal occipital tuber and Hopkins and Rothschild (1956), ignoring the subfamily, followed the same scheme and included a second monotypic genus, *Stephanopsylla* Rothschild, in this family. Smit (1982) astutely did not recognize this arrangement and placed Macropsyllinae in the family Hystrichopsyllidae (it is presumed that he also included *Stephanopsylla*, since there was mention of six genera in his family discussion). Lewis (1993, 1998) also followed this arrangement. Several observations substantiate the current systematic arrangement. Characters commonly shared by *Macropsylla* and other genera of the Hystrichopsyllidae include: 1) nearly a complete fusion of the distal arms of st. IX from base to apex; 2) presence of dual spermathecae; 3) combs or spinelets on one or more abdominal tergites; 4) anterior branch of tentorium visible; 5) apical tibial spur present; 6) mesopleural rod bifid (only slightly in *Typhloceras* Wagner); and 7) common pattern of femoral-tibial joint bristles (protibia, outer long, inner short, and meso- and metatibia, outer short, inner long). Smit (1982) indicated the absence of the anterior arm of the tentorium as a character to distinguish genera of the subfamily Macropsyllinae from those of Hystrichopsyllinae. Although the tentorium does not extend as far anteriorly in *Macropsylla* as it does in *Atyphloceras* Jordan and Rothschild, *Ctenoparia* Rothschild, *Hystrichopsylla* Taschenberg, and *Typhloceras,* it is visible. Specimens of *Stephanopsylla thomasi* (Rothschild) were not examined; however, illustrations of this monotypic genus appear morphologically similar to *Macropsylla* except for extreme modifications in the structure of the head. These similarities include an angular genal comb, mouth parts placed well behind the oral angle (lesser in *Macropsylla*), presence of abdominal

combs on t. II–V (*Macropsylla*) and t. I–VI (*Stephanopsylla*), presence of a dorsal occipital tuber, and a frons composed of a narrow frontal ridge separated by a narrow band (in lateral view) with a uniform row of minute setae along its posterior margin. These characters distinguish members of the Macropsyllinae from those of Hystrichopsyllinae.

Much emphasis has been placed on the importance of the occipital tuber (Oudemans 1909, Hopkins and Rothschild 1956). In addition to taxa belonging to Macropsyllinae, this structure is present in all genera of Stephanocircidae (minimally so in *Barreropsylla* Jordan). Wagner (1934) amply (and accurately) described the occipital tuber and other structures within the head capsule, using the stephanocircine *Plocopsylla enderleini* Wagner as a model. The nature of the occipital tuber can only be understood when viewed from a frontal or dorsal view (dissected specimens). The conventional lateral view of this structure might suggest that the apodeme is projecting centrally into the middle of the head, which is not the case. The structure is comprised of a heavily sclerotized ridge which follows the contour of the occiput adding rigidity and strength to the head capsule. The term occipital bridge might be more descriptive than occipital tuber. It is not surprising that sephanocircids possess it, since the structure of the head is highly modified to accommodate the helmet found in no other fleas [except the unrelated *Smitella thambetosa* (Pygiopsyllidae)]. Traub (1968) explained this convergent evolutionary condition in detail. Some members of Ischnopsyllidae also possess highly modified incrassations on the occipital areas of the head. One can only speculate why the occipital tuber occurs in relatively unrelated genera whose basic head structures are quite different. The peculiar shape of the frons in Macropsyllinae is reminiscent of some members of the family Ishnopsyllidae, but this feature is likely an independently convergent development. Hopkins

and Rothschild (1956) suggested the Ischnopsyllidae (and Stephanocircidae) might well have been descendents of "Macropsyllidae." Phylogenetic analysis of DNA sequence data does not support a close relationship between the Ischnopsyllidae and Macropsyllinae. These observations will be discussed in a future paper.

Both genera in the subfamily Macropsyllinae are restricted to the Australian subregion of the Australian Region. The isolated evolution of hystrichopsyllids (*Macropsylla* and *Stephanopsylla*) in Australia is puzzling considering the disjunct distribution of other hystrichopsyllids (*Atyphloceras, Ctenoparia, Hystrichopsylla* and *Typhloceras*). With exception of *Ctenoparia*, other genera of Hystrichopsyllidae are boreal inhabitants occurring in the Holarctic Region (*Hystrichopsylla, Atyphloceras*) and in the Palaearctic Region (*Typhloceras*). Although *Ctenoparia* and the two Australian genera share familial characteristics and early common geographical connections (Gonwanaland), they are quite dissimilar. It is evident that they were isolated very early or they were introduced by commensal murid rodents via human oceanic travels.

Jordan (1921) suggested that the difference in sizes of the two spermathecae of *Macropsylla* might be an evolutionary intermediate link between those genera possessing dual spermathecae and those with only one. Illustrations (Dunnet and Mardon 1974) of the female of *Stephanopsylla thomasi* and all specimens of *Macropsylla* that we examined demonstrate significant disparity in the shape and size of the paired spermathecae, whereas those of other genera (excluded from Australia) are consistently similar. Traub (1980) provided evidence that the Australian Hystrichopsyllidae (*Macropsylla* and *Stephanopsylla*) are the most ancient genera in the family. If this proves to be the case, one would expect the more primitive genera of the Hystrichopsyllidae (*Macropsylla* and *Stephanopsylla*) to possibly manifest greater morphological variability than more recently evolved taxa (*Atyphloceras, Ctenoparia, Hystrichopsylla,* and *Typhloceras*). Other than exteme modification of the head, *Stephanopsylla* is more similar to other hystrichopsyllids than *Macropsylla.* These similaries are noted particularly in the general features of t. IX, st. VIII, and the aedeagus. The extreme modification of the head of *Stephanopsylla* may be an evolutionary adaptation to its marsupial host species (Dasyuridae Goldfuss and Potoroidae Gray). *Stephanopsylla thomasi* has a peculiar disjunct distribution in Australia with a rather small number of specimens recorded from Western Australia and from Victoria, Australia. Additional collections are needed to elucidate the geographical distribution of *Stephanopsylla thomasi.*

The apparent preference of *Macropsylla* for murid rodents (*R. fuscipes* and *R. lutreolus*) is yet another indication of the systematic relationship to the Hystrichopsyllidae, as other genera in this family all share murid rodents as their preferred hosts. Dunnet and Mardon (1974) reported Australian fleas from 48 different genera of marsupials and only 12 genera of murid rodents. Records of *Macropsylla* occurring on marsupials are undoubtedly accidental associations. Divergence of the ancestral hystrichopsyllid likely occurred after introduction into Australia on murid rodents, some evolving after a successful transition to marsupial hosts (*Stephanopsylla*) while others continued evolving on murids (*Macropsylla*).

Acknowledgments

LITERATURE CITED

Dunnet, G. M. and D. K. Mardon. 1974. A monograph of Australian fleas (Siphonaptera). Australian Journal of Zoology, Supplementary Series No. 30, 273 pp.

Hocking, G. J. 1980. The occurrence of the New Holland mouse *Pseudomys novaehollandiae* (Waterhouse), in Tasmania. Australian Wildlife Research 7: 71–77.

Hopkins, G. H. E. and M. Rothschild. 1956. An Illustrated Catalogue of the Rothschild collection of fleas (Siphonaptera) in the British Museum. Vol. II, The British Museum (Natural History), London, 445 pp.

Jordan, K. 1921. A link between the double and single receptacula seminis of Siphonaptera. Ectoparasites 1: 127–128.

Lewis, R. E. 1993. Notes on the geographical distribution and host preferences in the Order Siphonaptera. Part 8. New taxa described between 1984 and 1990, with a current classification of the order. Journal of Medical Entomology 30(1): 239–256.

———. 1998. Résumé of the Siphonaptera (Insecta) of the world. Journal of Medical Entomology 35(4): 377–389.

Nowak, R. M. and J. L. Paridiso. 1983. Walker's mammals of the world. 4th Edition. Johns Hopkins University Press, Baltimore 2: 709–713.

Oudemans, A. C. 1909. Neue ansichten über die morphologie des flohkopfes, sowie über die ontogenie, phylogenie und systematik der flöhe. Novitates Zoologicae 12: 133–158.

Rothschild, M. and R. Traub. 1971. A revised glossary of terms used in the taxonomy and morphology of fleas. Trustees of The British Museum (Natural History), London, 85 pp.

Rothschild, N. C. 1905. Some new Siphonaptera. Novitates Zoologicae 12: 479–491.

Smit, F. G. A. M. 1982. Siphonaptera, pp. 557–562. In Parker, S. P., ed. Synopsis and classification of living organisms, Vol. 2. McGraw Hill, New York, 1,232 pp.

Traub, R. 1968. *Smitella thambetosa*, n. gen. and n. sp., a remarkable "helmeted" flea from New Guinea (Siphonaptera, Pygiopsyllidae) with notes on convergent evolution. Journal of Medical Entomology 5(3): 375–404.

———. 1980. The zoogeography and evolution of some fleas, lice and mammals, pp. 93–172. In Traub, R. and H. Starcke, eds. Fleas. Proceedings of the International Conference on Fleas. Ashton Wold/Peterborough, United Kingdom. A.A. Balkema, Rotterdam, The Netherlands, 420 pp.

Wilson, D. E. and D. M. Reeder. 1993. Mammal species of the world, a taxonomic and geographic reference. 2nd Edition. Smithsonian Institution Press, Washington, DC, 1,206 pp.

Wagner, J. 1934. Weitere beiträge zur auffassung des sogenannten "caput fractum" bei insecten (ber den kopfbau der "helmtragenden" flöhe). Zoologischer Anzeiger 106(1/2): 7–15.